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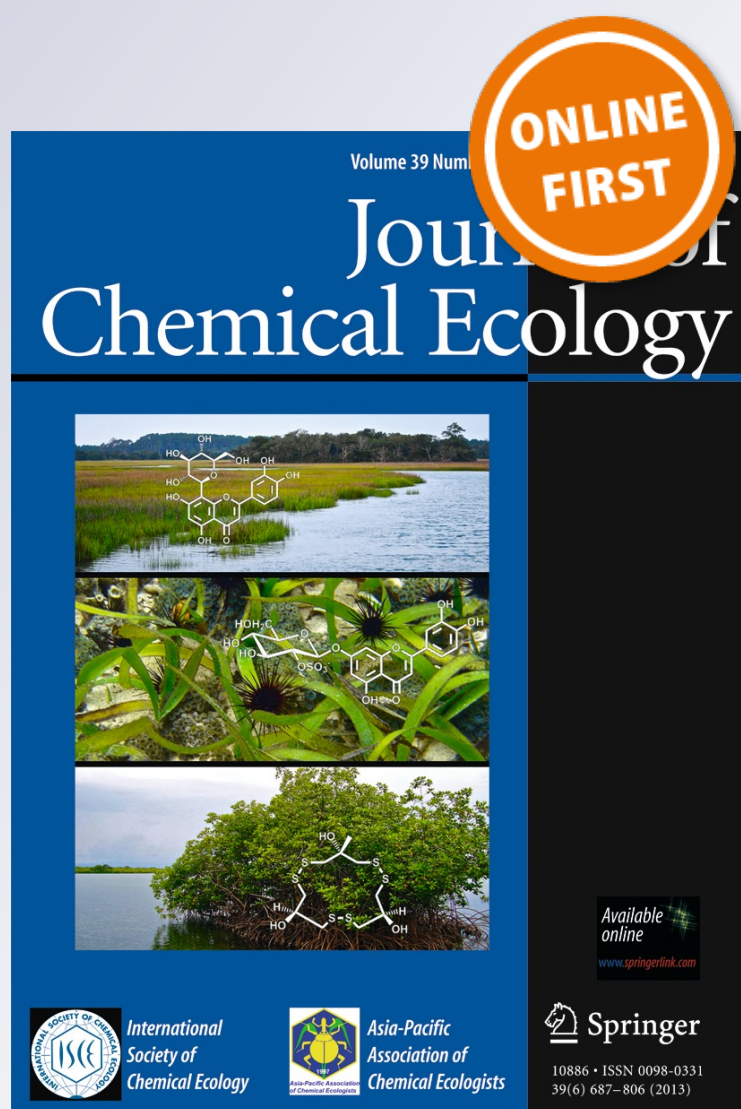
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Microbial Volatile Emissions as Insect Semiochemicals

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Abstract We provide a synthesis of the literature describing biochemical interactions between microorganisms and insects by way of microbial volatile organic compound (MVOC) production. We evaluated the functionality and ecological context of MVOC signals, and explored important metabolic pathways involved in MVOC production. The cosmopolitan distribution of microorganisms creates a context for frequent, and frequently overlooked, insect responses to microbial emissions. There are numerous instances of MVOCs being closely associated with insect feeding behaviors, but some MVOCs are also powerful repellants. Emissions from microorganisms *in situ* may signal aspects of habitat suitability or potential exposure to entomopathogens. In some ecosystems, bacterial or fungal volatiles can also incite insect aggregations, or MVOCs can resemble sexual pheromones that elicit mating and oviposition behaviors from responding insects. A single microorganism or MVOC can have different effects on insect behaviors, especially across species, ontogenies, and habitats. There appears to be a multipartite basis for insect responses to MVOCs, and complex tritrophic interactions can result from the production of MVOCs. Many biochemical pathways for behaviorally active volatile production by microbial species

are conserved across large taxonomic groupings of microorganisms. In addition, there is substantial functional redundancy in MVOCs: fungal tissues commonly produce polyketides and short-chain alcohols, whereas bacterial tissues tend to be more commonly associated with amines and pyrazines. We hypothesize that insect olfactory responses to emissions from microorganisms inhabiting their sensory environment are much more common than currently recognized, and that these signals represent evolutionarily reliable infochemicals. Insect chemoreception of microbial volatiles may contribute to the formation of neutral, beneficial, or even harmful symbioses and provide considerable insight into the evolution of insect behavioral responses to volatile compounds.

Keywords Attraction · Microbes · Yeast · Fungi · Bacteria · Insect behavior · Signaling · Orientation · Pheromones · Volatile organic compounds · Tritrophic interaction

Introduction

Microbes are intertwined with the foundations of life on Earth (Nisbet and Sleep 2001) and have existed for billions of years (Elena and Lenski 2003). However, in an ecological sense, many previous explorations of microbial functions in nature were limited to select roles – primarily as recyclers of nutrients (Janzen 1977; McCarthy and Williams 1992), while their applications in entomology often have been relegated to biological control of pest insect species (Hajek et al. 2007).

Historically, the treatment of microbial ecology by entomologists has been narrow in scope, and this was primarily due to technological limitations: researchers were limited to working with microorganisms that could be collected in the field and cultured on artificial medium in the laboratory. The establishment of new sequencing technologies (Shendure and Ji 2008) are allowing for identification and ecological

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classification of previously unstudied insect-microbe associations (Hugenholtz et al. 1998): transcriptomics, proteomics, and metabolomics allow for analyses of microbial functions in their natural environment (Xu 2006). The concurrent development of mathematical models and enhanced computing power has enabled researchers to analyze complex data sets and produce results with greater interpretive value than in previous decades.

One potential pathway for ecologically relevant associations between insects and microorganisms to develop is through insect chemoreception of microbial emissions, with microbial emissions utilized as infochemicals. Insects have evolved complex chemosensory systems that are extremely sensitive to volatile chemical signals, although variety of gustatory, tactile, and visual cues also moderate insect behaviors. Yet, olfaction is the single most studied means of insect chemoreception. Many insects are especially sensitive to odors that advertise nutrient resources, competitors, predators, potential mates, and habitat suitability (Price et al. 2011), and in many ecosystems, signalers and the intended receivers are not the only participants involved in deciphering chemical signaling. Often, unintended “eavesdropping” results in various forms of exploitation of infochemicals (Endler 1993) and diffuse symbiotic associations (Johnstone 2002).

The production of volatile compounds by microorganisms such as bacteria and fungi are commonplace, and the aromas produced by microbes in food products have long been selected for human preferences, as is the case with fermented foods such as cheese, wine, beer, and yogurt. Yet, although the power that odor has to influence animal behavior has been long recognized, relatively little thought has been given to microbial sources of odor, or how organisms may have evolved to exploit microbial volatile organic compounds (MVOCs) as behavioral cues.

Much of the applied research on MVOCs focuses on MVOCs as indicators of contamination and pollutants with potential consequences for human health (Pasanen et al. 1998; Wessen and Schoeps 1996). However, there are numerous examples where MVOCs have ecological functions. For instance, some MVOCs attract or repel insects, inhibit the growth of microorganisms competing with associated insects, stimulate oviposition, mimic plant hormones, or even induce plant resistance (Davis et al. 2011; Ryu et al. 2003, 2004). The above cases describe only a fraction of the complexity associated with MVOCs, and here we explore some MVOC functions underlying insect behavioral responses. We posit that the interactions described here may be broadly extendable to insects and microorganisms in many ecosystems, and that there likely are evolutionary patterns underpinning insect attraction to specific MVOCs. Due to the broad scope of insect-microbe interactions, we focus on exploring the roles of MVOCs as mediators of insect behavior. The term ‘microbe’ is used throughout in reference to both bacteria and fungi, although

we note that many multicellular fungi may be much larger than the insects associated with their odors. Although it is not possible to review the entirety of this field here, we make an effort to cover nearly all seminal works on insect responses to emissions from bacterial and fungal sources.

A Need for Further Investigation of Microbial Volatile Emissions in Insect Behavioral Ecology Ecologists are quickly realizing that insects are highly responsive to microbial emissions (Ezenwa et al. 2012): microbially-mediated insect attraction (Chaudhury et al. 2010; Lowery et al. 2008; Ma et al. 2012; Tomberlin et al. 2012a, b), repellence (Burkepile et al. 2006), and even aberrant behaviors (Fujiyuki et al. 2004; George et al. 2013; Hughes et al. 2011) not conducive to the survivorship of the insect itself have been demonstrated. Additionally, in some cases, microbial associates are responsible for important physiological (Haine et al. 2008; Rozen et al. 2008) functions of insects, and insect-microbe interactions may even play a role in quorum sensing (Lowery et al. 2008; Ma et al. 2012; Tomberlin et al. 2012a, b)

Despite the importance of microbial species in insect life-histories, integration between chemical and microbial ecology in basic and applied entomology is just beginning to receive appropriate attention. However, combining these approaches in entomological research may yield novel approaches to identifying insect semiochemicals, and elucidating the factors that shape insect responses to behavioral cues. Here, we explore the literature relating MVOCs to insect behavior, and ask some basic questions about interkingdom chemical signaling: (1) What do MVOCs signal to insects? (2) How generalizable are insect olfactory responses to MVOCs? (3) What role do MVOCs play in tritrophic interactions? (4) Which metabolic pathways are involved in MVOC production?

What Do Microbial Emissions Signal?

A single infochemical can have multiple functions, and the bioactivity of any individual MVOC in the context of insect chemoreception likely varies with respect to insect species, ontogeny, habitat, and environmental conditions. Although a multitude of insect responses to MVOCs are possible, we focus on how MVOCs mediate attraction to mating opportunities, oviposition sites, and food resources, as well as their roles in eliciting avoidance behaviors or signaling environmental hazards (Table 1).

Aggregation Pheromones

Wertheim et al. (2005) noted that a striking number of insects that exhibit aggregation behaviors are strongly associated with specific microbial communities, although few researchers have treated MVOCs directly as pheromonal communications. Furthermore,

Table 1 A list of microorganisms, the volatiles produced by cultures or inoculum, and the insects that explicitly responded to volatiles; including reference to the published work that investigated the insect-microbial association. Insect behaviors were categorized as (experimentally demonstrated) attraction to or avoidance of microbial odors; and microbial odors emanated directly from cell cultures, filtrates, or food/plant material inoculated with microbial tissue.

Microbial species	Volatiles produced	Insects responding to volatiles	References
<i>Ambrosiomyia</i> sp. (F); <i>Ambrosiella xylebori</i> (F); <i>Raffaelea lauricola</i> (F)	Not determined	<i>Xyleborus glabratus</i> ; <i>Xyleborus ferrugineus</i> (Coleoptera:Curculionidae); <i>Xylosandrus crassisculus</i> ; <i>Xyleborinus saxesenii</i> (Coleoptera:Curculionidae)	Huler et al. 2011
<i>Amylostereum</i> sp. (F)	Acetaldehyde	<i>Ibalia leucospides</i> (Hymenoptera:Ibalidae); <i>Rhyssa persausoria</i> (Hymenoptera:Inciseumonidae); <i>Megarhyssa nortoni</i> (Hymenoptera:Inciseumonidae)	Madden 1968
<i>Aspergillus nidulans</i> (F)	Not determined	<i>Folsomia candida</i> ^a (Entomobryomorpha:Isotomidae)	Rohlfis et al. 2007
<i>Aspergillus sydowii</i> (F); <i>Aspergillus versicolor</i> (F)	1-octen-3-ol	<i>Lariophagus distinguendus</i> (Hymenoptera:Peromalidae)	Steiner et al. 2007a, b
<i>Aureobasidium pullulans</i> (Y/F)	2-methyl-1-butanol; 3-methyl-1-butanol; 2-phenylethanol	<i>Vespula pennsylvanica</i> ; <i>Vespula germanica</i> (Hymenoptera:Vespidae) <i>Eupodes volucris</i> <i>Sphaerophoria</i> spp. (Diptera: Syrphidae)	Davis et al. 2012a, b; Davis and Landolt 2013
<i>Beauveria bassiana</i> (F)	Not determined	<i>Anopheles stephensi</i> (Diptera:Culicidae) <i>Anthocoris nemorum</i> (Hemiptera:Anthocoridae); <i>Macrotermes michealseni</i> (Isoptera:Termitidae)	Meyling and Pell 2006; Mburu et al. 2012; George et al. 2013
<i>Candida krusei</i> (Y)	Not determined	<i>Carpophilus lugubris</i> (Coleoptera:Nitidulidae)	Blackmer and Phelan 1991
<i>Candida shehatae</i> (Y); <i>C. guillemondii</i> (Y)	Ethanol; acetaldehyde; 2-methyl-1-propanol; 1-propanol; ethyl acetate; 3-methyl-1-butanol; 2-methyl-1-butanol; 3-hydroxybutanone	<i>Carpophilus humeralis</i> (Coleoptera:Nitidulidae)	Nout and Bartelt 1998
<i>Candida sonorensis</i> (Y); <i>Pichia cactophila</i> (Y); <i>Cryptococcus albidus</i> (Y)	Not determined	<i>Drosophila buzzatii</i> ; <i>Drosophila aldrichi</i> (Diptera: Drosophilidae)	Barker et al. 1981a; Barker et al. 1981b
<i>Citrobacter freundii</i> (B); <i>Klebsiella pneumoniae</i> (B)	2-pentanone; 3-methylbutanamine; pyrazine; 3-methyl-1-butanol; 2-methyl-1-butanol; dimethyldisulfide; 2-hexanone; 2,3,4,5-tetrahydropyridine; methylpyrazine; 2,5-dimethylpyrazine; benzaldehyde; trimethylpyrazine; 2-ethylhexanol; 2-phenylethanol; 1-phenyl-2-propanone; 2-butanone; 3-methylbutanal; phenol	<i>Anastrepha ludens</i> (Diptera:Tephritidae)	Robacker and Bartelt 1997
<i>Cladosporium cladosporioides</i> (F); <i>Cladosporium herbarum</i> (F); <i>Penicillium spinulosum</i> (F)	nonanone; α -pinene; phenylethanol; decane; dipentene; decanal	<i>Orchesella cincta</i> ^a (Entomobryomorpha:Entomobryidae); <i>Tomocerus flavescens</i> ^a (Entomobryomorpha:Tomoceridae)	Hedlund et al. 1995
<i>Coriaria versicolor</i> (F); <i>Ganoderma adspersum</i> (F); <i>Piptoporus betulinus</i> (F)	1-octen-3-ol; (R)-curcumen; α -cedrene	<i>Octotennus glabriculus</i> (Coleoptera:Cidae); <i>Cis boleti</i> ; <i>Cis nitidus</i> ; <i>Cis bilamellatus</i> (Coleoptera:Cidae)	Guevara et al. 2000
<i>Donkiosporia expansa</i> (F)	Not determined	<i>Xestobium rufivillosum</i> (Coleoptera:Anobiidae)	Belmain et al. 2002
SJB-133 (<i>Entomocorticium</i> sp. A) (F)	Verbenone; <i>cis</i> -verbenol; <i>trans</i> -verbenol; myrtenol	<i>Dendroctonus frontalis</i> (Coleoptera:Curculionidae)	Brand et al. 1975; Brand et al. 1976

Table 1 (continued)

Microbial species	Volatiles produced	Insects responding to volatiles	References
<i>Epichloë typhina</i> (F); <i>Epichloë sylvatica</i> (F)	Chokol K	<i>Botanophila</i> spp. (Diptera:Anthomyiidae)	Schiesti et al. 2006
<i>Fomes fomentarius</i> (F); <i>Fomitopsis pinicola</i> (F)	<i>rac</i> -1-octen-3-ol	<i>Malthodes fuscus</i> (Coleoptera:Cantharidae); <i>Epinothia tedella</i> (Lepidoptera:Tortricidae); <i>Anaspis marginicollis</i> ; <i>Anaspis rufilabris</i> (Coleoptera:Scaphitidae); <i>Cis glabratus</i> ; <i>Cis quadridens</i> (Coleoptera:Ciidae); <i>Emnearthron comutum</i> (Coleoptera:Ciidae)	Jonsell and Nordlander 1995; Fäldt et al. 1999
<i>Hansenula capsulata</i> (Y); <i>Pichia pinus</i> (Y)	Verbenone	<i>Dendroctonus ponderosae</i> (Coleoptera:Curculionidae)	Hunt and Borden 1990
<i>Hansenula holstii</i> (Y)	3-methyl-1-butanol; 3-methylbutyl ethanoate; 2-phenylethanol; 2-phenylethyl acetate	<i>Dendroctonus frontalis</i> (Coleoptera:Curculionidae)	Brand et al. 1977
<i>Klebsiella oxytoca</i> (B); <i>Bacillus</i> spp. (B)	Dialkyl sulphides	<i>Diadromus pulchellus</i> (Diptera:Ichneumonidae)	Thibout et al. 1993; Thibout et al. 1995
Not determined (F)	Not determined	<i>Fannia canicularis</i> (Diptera:Fanniidae)	Dindonis and Miller 1981
Not determined (F); multiple species	Not determined	<i>Tribolium castaneum</i> (Coleoptera:Tenebrionidae)	Ahmad et al. 2012
Not determined (F)	Not determined	<i>Diachasma morpha longicaudata</i> (Hymenoptera: Braconidae)	Segura et al. 2012
<i>Mortierella isabellina</i> (F); <i>Verticillium bulbiliosum</i> (F)	2-methyl-1-propanol; 2-pentanol; 3-methyl-1-butanol; 1-heptene; α -pinene; 1-phenylethanol; 2-octene; 1-octen-3-ol; γ -octalone; dipentene; 1-octanol; 1-methylphenylethanol; decanal; camphor	<i>Onychiurus armatus</i> ^a (Poduromorpha:Onychiuridae)	Bengtsson et al. 1991
<i>Muscodor vitigenus</i>	Napthalene	<i>Cephus cinctus</i> (Diptera:Cephidae)	Daisy et al. 2002
<i>Ophiostoma minus</i> (F)	Not determined	<i>Roctrocus xylophagorum</i> (Hymenoptera:Pteromalidae); <i>Spathius pallidus</i> (Hymenoptera: Braconidae)	Sullivan and Berisford 2004
<i>Ophiostoma ips</i> (F); <i>Burkholderia</i> sp. (B); <i>Pichia scolyti</i> (Y)	Not determined	<i>Heydenia unica</i> (Hymenoptera:Pteromalidae); <i>Medetera</i> sp. (Diptera:Dolichopodidae); <i>Dolichopodidae</i> sp. (Diptera:Dolichopodidae)	Boone et al. 2008
<i>Pantoea</i> (<i>Enterobacter</i>) <i>agglomerans</i> (B)	3-methyl-1-butanol; 3-hydroxybutanol; 2-phenylethanol; 2,5-dimethylpyrazine; trimethylpyrazine; dimethylsulfoxide; ammonia, indole	<i>Anastrepha ludens</i> ; <i>Anastrepha suspensa</i> (Diptera:Tephritidae); <i>Rhagoletis mendax</i> ; <i>Rhagoletis pomonella</i> (Diptera:Tephritidae); <i>Schistocerca gregaria</i> (Orthoptera:Acrididae)	Epsky et al. 1998; Lauzon et al. 1998; Dillon et al. 2000; Robacker and Lauzon 2002; Robacker et al. 2004; MacCollom et al. 2009
<i>Phoma</i> spp. (F); <i>Fusarium</i> spp. (F); <i>Rhizopus</i> spp. (F)	Dimethyl trisulfide; 2-phenylethanol	<i>Musca domestica</i> (Diptera:Muscidae)	Lam et al. 2010
<i>Penicillium corymbiferum</i> (F); <i>Scopulariopsis brevicaulis</i> (F); <i>Fusarium</i> sp. (F)	1-octen-2-one; (<i>R, S</i>)-3-octanol; 3-octanol; 3-methyl-1-butanol; 2-phenylethanol; ethanol	<i>Oryzaephilus surinamensis</i> ; <i>Oryzaephilus mercator</i> (Coleoptera:Silvanidae); <i>Cryptolestes ferrugineus</i> (Coleoptera:Laemophloeidae); <i>Ahasverus advena</i> (Coleoptera:Silvanidae); <i>Cathartus quadricollis</i> (Coleoptera:Silvanidae)	Dolinski and Loschiavo 1973; Pierce et al. 1991
<i>Penicillium expansum</i> (F)	3-methylanisole	<i>Hylobius abietis</i> (Coleoptera:Curculionidae)	Azeem et al. 2013
	Not determined	<i>Conogethes punctiferalis</i> (Lepidoptera:Crambidae)	Honda et al. 1988

Table 1 (continued)

Microbial species	Volatiles produced	Insects responding to volatiles	References
<i>Penicillium</i> sp. (F); <i>Cladosporium</i> sp. (F); <i>Aspergillus fumigatus</i> (F); <i>Mucor</i> sp. (F); <i>Endothia parasitica</i> (F); <i>Alternaria solani</i> (F)	2-Methylpropan-1-amine	<i>Lucilia sericata</i> (Diptera:Callophoridae)	Ma et al. 2012
<i>Proteus mirabilis</i> (B)	Not determined	<i>Bradysia impatiens</i> (Diptera:Sciaridae)	Braun et al. 2012
<i>Pythium ophanidermatum</i> (F); <i>Pythium irregular</i> (F); <i>Pythium ultimum</i> (F)	Acetaldehyde; ethanol; 1-butanol; 1-propanol; 2-methyl-1-propanol; 2,3-butanediol; 2-methyl-1-butanol; 3-methyl-1-butanol; ethyl hexanoate; acetoin; ethyl octanoate; acetic acid; ethyl decanoate; 2-phenylethanol; ethyl acetate; isopentyl acetate	<i>Carpophilus hemipterus</i> ; <i>Carpophilus humeralis</i> ; <i>Carpophilus lugubris</i> (Coleoptera:Nitidulidae); <i>Drosophila melanogaster</i> (Diptera:Drosophilidae); <i>Rhodnius prolixus</i> (Hemiptera:Reduviidae); <i>Triatoma infestans</i> (Hemiptera:Reduviidae)	Wildman 1933; Phelan and Lin 1991; Lin and Phelan 1991; Guerenstein et al. 1995; Nout and Bartelt 1998; Lorenzo et al. 1999; Becher et al. 2012
<i>Saccharomyces cerevisiae</i> (Y)	Not determined	<i>Spodoptera exigua</i> (Lepidoptera:Noctuidae); <i>Cotesia marginiventris</i> (Hymenoptera:Braconidae)	Cardoza et al. 2003
<i>Sclerotium rolfsii</i> (F)	Ammonia; trimethylamine; isoamylamine; 2-methyl-butylamine; 2,5-dimethylpyrazine; acetic acid	<i>Anastrepha ludens</i> (Diptera:Tephritidae)	Robacker and Moreno 1995; Robacker and Flath 1995
<i>Staphylococcus aureus</i> (B)	1-butanol; 2,3-butanedione; 2-hydroxy-3-pentanone; 2-methyl-1-butanol; 2-methylbutanal; 2-methylbutanoic acid; 3-hydroxy-2-butanone; 3-methyl-1-butanol; 3-methylbutanal; 3-methylbutanoic acid	<i>Anopheles gambiae</i> (Diptera:Culicidae)	Verhulst et al. 2009; Verhulst et al. 2011
<i>Staphylococcus epidermidis</i>	Propanone; 2,3-butanedione; 3-hydroxy-2-butanone; 3-methyl-1-butanol; 3-methyl-2-butanal; butanoic acid; 3-methylbutanoic acid; 2-methylbutanoic acid; 2,5-dimethylpyrazine; benzeneethanol	<i>Episyrphus balteatus</i> (Diptera:Syrphidae)	Leroy et al. 2011b
<i>Staphylococcus sciuri</i> (B)	<i>cis</i> - and <i>trans</i> -octa-1,5-dien-3-ol	<i>Tyrophagus putrescentiae</i> ^b (Sarcoptiformes:Acaridae)	VanHaelen et al. 1980

^a Collembola

^b Arachnida

the role of aggregations pheromones can vary. For example, pheromones may signal food sources, oviposition sites, or mating opportunities, so it will be important to distinguish the specific function of MVOCs in relation to aggregative behaviors. Several insects possess aggregation pheromones that are released by or in association with fungal and bacterial symbionts (Tillman et al. 1999; Wertheim et al. 2005).

Bark beetles (Coleoptera: Curculionidae) have a variety of gut symbionts capable of producing compounds that are used as pheromones by their host. Hunt and Borden (1990) reported that two yeasts, *Hansenula capsulata* Wickerham, and *Pichia pini* (Holst) Phaff, associated with the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytinae), are capable of producing the anti-aggregation pheromone verbenone, which the yeasts convert from *cis*- and *trans*-verbenol produced by female beetles. These beetles appear to rely on microbial symbionts for signals about subcortical population density, and MVOCs play a role in terminating aggregation and mass attack on individual host trees. Similar processes may occur in other bark beetles systems (i.e., southern pine beetle and mycangial fungi, Brand et al. 1976; spruce beetle and yeast *Candida nitrophila*, Leufven et al. 1984). Conversely, there also is evidence that gut bacteria do not play a significant role in pheromone production for some bark beetles (Blomquist et al. 2010). Additionally, microbial associates of bark beetles may contribute indirectly to MVOC production by providing nutrients or precursory compounds required for the synthesis of beetle pheromones. For instance, Bentz and Six (2006) show that the mutualistic fungus *Grossmania clavigera* produces sterols that are required for the biosynthesis of aggregation pheromones by *D. ponderosae* females.

Similarly, Dillon et al. (2000) showed that a component of the locust pheromone, guaiacol, derived from locust fecal pellets promotes locust mating aggregations. Guaiacol is produced mainly by bacteria (*Pantoea agglomerans*, among others) found in the locust gut. Gut bacteria also help the locust defend against microbial pathogens by producing antimicrobial phenolic compounds (Dillon et al. 2002). Guaiacol also is known to be synthesized by millipedes and Hemiptera (Duffey et al. 1977). In addition, Hoyt et al. (1971) found an undefined bacterium isolated from the collateral glands of the female grass grub beetle, *Costelytra zealandica* White (Coleoptera: Scarabaeidae) that produced phenol and attracts male beetles.

Oviposition Stimulants

Insects rely heavily on olfactory cues to locate and select oviposition sites, and olfactory signals may advertise relevant information concerning the suitability of sites. Colonization of host material by microorganisms often modifies volatile emissions (Tasin et al. 2011), and insect oviposition preferences are known to be related to MVOCs associated

with insect digestive tracts or frass as well (Dillon et al. 2002).

The oviposition behaviors of dipterans are adaptable in response to MVOCs. For instance, MVOCs produced by the bacteria *Enterobacter agglomerans* increase oviposition rates of the apple maggot fly, *Rhagoletis pomonella* Walsh (Diptera: Tephritidae), on fruit (Lauzon et al. 1998). Likewise, Chaudhury et al. (2010) noted that blood inoculated with bacteria isolated from the screwworm, *Cochliomyia hominivorax* Coquerel (Diptera: Calliphoridae) from infested animal wounds was an attractive oviposition site for adult flies. Similarly, tsetse flies, *Glossina* spp. (Diptera: Muscidae) are attracted to typical fungal odors such as 1-octen-3-ol (Steiner et al. 2007a) that are also associated with many mammals. Interestingly, 1-octen-3-ol (mushroom alcohol) is attractive to many insect species (de Bruyne and Baker 2008), suggesting that attraction to this common MVOC has evolved independently in different insect species numerous times. Oviposition preferences of the Australian sheep blow fly, *Lucilia cuprina* L. (Diptera: Calliphoridae) are mediated by MVOCs: Emmens and Murray (1983) demonstrated that sheep fleeces (wool) inoculated with *Pseudomonas aeruginosa* were more attractive oviposition sites and increased egg laying by *L. cuprina*. Bacterial volatiles also affect oviposition rates by the stable fly, *Stomoxys calcitrans* L. (Diptera: Muscidae) and a strain of *Citrobacter freundii* strongly stimulated oviposition by gravid females as well as supported the development of larval flies (Romero et al. 2006). The authors speculated that bacterial volatiles were particularly important for signaling the relative suitability of oviposition sites for larval developmental success.

MVOCs also are well known oviposition stimulants for many mosquito species (Lindh et al. 2008); although Huang et al. (2004) demonstrated that emissions from bacteria also can repel gravid mosquitoes. Gravid *Aedes aegypti* L. (Diptera: Culicidae) mosquitoes use volatiles in the form of carboxylic acids and methyl esters emitted from alpha and gamma proteobacteria to direct egg laying in favorable habitats (Ponnusamy et al. 2008, 2010). There also is evidence that bacteria, or water-soluble compounds secreted by bacteria, stimulate hatching of *A. aegypti* eggs (Ponnusamy et al. 2011). Skin-dwelling bacteria on mammals and birds are also known to affect host preferences and settling behavior of the malarial vector, *Anopheles gambiae* Giles (Diptera: Culicidae) (Verhulst et al. 2009). Likewise, Trexler et al. (2003) found that gravid *Aedes albopictus* Skuse (Diptera: Culicidae) oviposited more frequently in water that was inoculated with *Psychrobacter immobilis*, *Sphingobacterium multivorum*, or an unidentified *Bacillus* species, and that the volatiles collected from these bacterial species elicited electroantennographic responses. However, MVOCs also can deter mosquito oviposition: Huang et al. (2004) demonstrated that a mixture of bacteria originating from a natural larval habitat, containing *Pseudomonas*, *Stenotrophomonas*, *Enterobacter*, *Pantoea*, *Klebsiella*, *Acinetobacter*, *Aeromonas*,

and *Bacillus* reduced oviposition in gravid *A. gambiae*, thus suggesting that communities, rather than individual bacteria species, are essential for releasing the MVOC complexes needed to elicit oviposition.

Tasin et al. (2012) found that oviposition preferences of the grapevine moth *Lobesia botrana* Schiff. (Lepidoptera: Tortricidae) relates to the nutritional value of the microorganisms (i.e., yeasts are better than bacteria, and bacteria are better than filamentous fungi) that can be found on host grape vines. The odors released by grape-born yeasts positively affect moth oviposition. In contrast, volatiles from some bacteria and phytopathogenic fungi can deter moth oviposition. For instance, Honda et al. (1998) showed that the presence of bacteria rather than fungi inhibited oviposition by gravid yellow peach moths, *Conogethes punctiferalis* Guenée (Lepidoptera: Pyralidae) on codling fruit, again indicating that the presence of volatiles from a specific microbial community may be a critical cue for eliciting oviposition. Interestingly, the presence of phytopathogenic fungi on fruit was more attractive to the yellow peach moth for oviposition substrates than on a fresh codling (Honda et al. 1998).

Host Location and Attraction to Food Resources

Insect representatives from all major insect groups have close associations with symbiotic microorganisms that provide essential nutrients themselves or attract insects to the food source on which the microbe is growing. Many insects specifically employ MVOCs to locate food sources (DeVries 1987) such as nectar, fruit, decomposing tree or animal tissues, weakened organisms, or material resources. For instance, fermented fruit is attractive to many insect species (Utrio and Eriksson 1977), and many compounds from fermented fruit are known insect attractants or pheromone compounds: ethyl acetate, ethyl hexanoate, and phenylethanol are volatile products of fermented fruit, as well as sexual pheromones for insects such as the medfly *Ceratitis capitata* Wied (Diptera: Tephritidae) (Jang et al. 1994), death's head cockroach *Blaberus discoidalis* Audinet-Serville (Dictyoptera: Blaberidae) (Brossut et al. 1974), and the flounced chestnut moth *Agrochola helvola* L. (Lepidoptera: Noctuidae) (Bestmann et al. 1977).

Diptera For the onion fly, *Delia antiqua* (Anthomyiidae), microbial decomposition of plant tissues enhances larval survival and developmental rates. Female flies inoculate host onion material during feeding and oviposition, coat their eggs with microorganisms, and preferentially oviposit on bacteria-infested plants (Hausmann and Miller 1989). The microbes are thought to predispose healthy onions to more successful to subsequent attacks by larvae, because healthy onions cannot be penetrated by larvae (Finch and Eckenrode 1985), or provide limiting nutrients that enhance larval survival (Judd and Borden 1992). This is similar for *Drosophila* (Diptera:

Drosophilidae) fruit flies, in which adults inoculate breeding substrates with yeasts, which improves the resource for larval feeding (Begon 1986). A recent report by Becher et al. (2012) revealed that yeast volatiles, rather than fruit volatiles, were principally responsible for the attraction of *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) to food resources, and *D. melanogaster* is known to vector the same yeasts it is attracted to (Stamps et al. 2012).

Several dipteran predators use MVOCs to locate prey insect species. In a bark beetle system (*Ips pini*), a predaceous *Medetera* spp. (Diptera: Dolichopodidae) is highly attracted to wood material inoculated with either the fungus *Ophiostoma ips* or a bacterial strain (*Burkholderia* sp., Boone et al. 2008).

Necrophagous flies are important colonizers of decaying organic resources, and as such, are highly responsive to MVOCs from decaying carcasses. Carrion flies use sulphide compounds emitted by bacteria to identify rotting carcasses for oviposition (Stensmyr et al. 2002). They often appear in a predictable sequence in response to chemical cues emanating from decaying host material (Pelosi et al. 2006; Reinhard 2004), but the sources of those aromatics are not always known. Frederickx et al. (2012b) explored the VOCs released by cadavers. Through electroantennography and olfactory behavioral assays, they determined that the blow fly, *Lucilia sericata* Meigen (Diptera: Calliphoridae), responded to dimethyl disulfide, putrescine, butan-1-ol, and that, in general, females were more sensitive than males. Further work determined that the blow fly pupae and larvae released VOCs (Frederickx et al. 2012a); however, it was unclear whether the source was directly from the insects or from the microbes which inhabit the insect. The authors noted that bacteria from the microbial families Pseudomonaceae, Enterobacteriaceae and Bacillaceae emit compounds similar to those collected from insect larvae and pupae, which could indicate that the attractive volatiles were from microbial sources. Pupal casings also have been shown to be an important source of volatile emission, but it is not yet known whether microbes contribute to the emission profile (Zhu et al. 2006).

As discussed in the previous section (Oviposition Stimulants), mosquitos must differentiate specific odors or blends of odors from the multitude of VOCs found in their environment in order to locate suitable hosts. Mosquitoes use the volatiles produced by bacteria on human skin to locate feeding sources (Verhulst et al. 2009), but, they are selective about the bacteria they respond to when seeking a human host on which to feed. *Pseudomonas aeruginosa* is present on the human skin; and it is also a common environmental bacterium. *Anopheles gambiae* Giles was not attracted to the compounds emitted by *P. aeruginosa*, but was attracted to VOCs from *Corynebacterium* spp. and *Brevibacterium* spp. (Verhulst et al. 2010a, b). Both of the attractive bacteria are more strongly correlated with human skin than the surrounding environment, implying that volatiles from these bacterial

sources may be more evolutionarily reliable chemical signals than the ubiquitous *P. aeruginosa*. In addition, the physiological state of the insect impacts its response to particular MVOCs, thus demonstrating the precision and delicate balance of these interkingdom signaling (Tomberlin et al. 2012b).

Hymenoptera Davis et al. (2012a) found volatile emissions from an epiphytic microbe have semiochemical activity for vespid wasps (Hymenoptera: Vespidae). The yellowjacket wasps *Vespula pennsylvanica* Sauss. and *Vespula germanica* (F.) consistently vectored the fungus *A. pullulans* and were attracted to volatiles release by the fungus. They hypothesized that microbes that produce volatiles from the metabolism of complex sugars (fermentation pathways) could signal suitable nutrient sources to foraging wasps.

Additionally, many hymenopteran parasitoids use MVOCs associated with living prey to locate food sources for their offspring (De Moraes and Mescher 1999; Turlings and Benrey 1998). For example, the hymenopteran parasitoids of wood-infesting larvae, such as bark beetles (Lieutier et al. 2004; Solheim 1992) and wood wasps (Madden 1968) employ MVOCs from the bacterial and fungal symbionts of wood-boring insects to locate hosts. The abundance and location of microorganisms within tree hosts influence the strength of volatile signals (Boone et al. 2008). For example, fungi (e.g., *Ophiostoma ips* associated with bark beetles in the genus *Ips*) may produce a stronger signal and be important in long distance host location by parasitoids, while bacteria and yeast may be important in short distance location (Boone et al. 2008). Ryan et al. (2012) found that the wood wasp *Sirex noctilio* F. (Hymenoptera: Siricidae) strongly avoided host material colonized by the bark-beetle vectored fungi *Leptographium wingfeldii* in assays that tested olfactory cues—indicating that insects with similar life-histories may use MVOCs to partition host resources and minimize competitive interactions. Similarly, the parasitic wasp *Lariophagus distinguendis* Forster (Hymenoptera: Pteromalidae) avoided fecal pellets from host beetles [*Sitophilus granarius* L. (Coleoptera: Curculionidae)] and wheat plants that were colonized with the filamentous fungi *Aspergillus sydowii* and *A. versicolor*. Interestingly, the authors found that the primary fungal volatile responsible for repellency was 1-octen-3-ol (Steiner et al. 2007a).

Lepidoptera Microbes are key to the fermentation odors in nectar and fruit (Herrera et al. 2008; Raguso 2004), which are attractive to many adult Lepidoptera and Hymenoptera. Noctuids, geometrids, tortricids, and pyralids are major lepidopteran groups that have been repeatedly demonstrated to be attracted to fermenting fruit. Of the many compounds released, the most commonly present are esters (El-Sayed et al. 2005). El-Sayed et al. (2005) tested fermented sugar baits and found that over 90 % of the species caught were noctuid moths (Noctuidae). In support of a microbially-mediated hypothesis for moth attraction to hosts, Herrera et al. (2008) found that complex and abundant microbial communities occur in nectar

sources. However, yeast communities in nectar can become sufficiently dense, reducing or altering nectar sugar composition so as to ultimately decrease nectar attractiveness. Alternatively, microbes may enhance the aroma or volatile components of rotting fruit or flowers making them more attractive to lepidopteran visitors (DeVries 1987).

Furthermore, herbivorous lepidoptera may use information from MVOCs to select host plants, and olfactory cues provide lepidopteran herbivores information about the health status of host plants (Tasin et al. 2012). Recently, Witzgall et al. (2012) described a mutualism between the codling moth, *Cydia pomonella* L. (Lepidoptera: Tortricidae), and two common nectar-living yeasts, *Metschnikowia anaduensis* and *M. pulcherima*. They discovered that fermentation volatiles produced by yeast cultures were attractive to *C. pomonella* and could elicit upwind orientation and electroantennographic responses by moths, as well as enhance larval growth rates. This report is one of the first demonstrating a mutualism based on the production of volatiles by microbial species, though there are likely many similar associations that are as of yet undiscovered.

Coleoptera Phelan and Lin (1991) found that bananas inoculated with the yeast *Saccharomyces cerevisiae* attracted twice as many dried-fruit beetles, *Carpophilus hemipterus* L. (Coleoptera: Nitidulidae) as aseptic bananas. Their results suggest that this generalist beetle locates its hosts by a long-range response to a variety of fruit volatiles, whose concentrations are enhanced by fungal decomposition. Nitidulid beetles (Coleoptera: Nitidulidae) are attracted to MVOCs associated with fermenting substrates such as overripe fruit (Nout and Bartelt 1998) and are reported to inoculate fruit-degrading yeasts onto host material (Michailides et al. 1992). Aggregative behavior by the beetles may enhance inoculation success and render the fruit more suitable for larval development (Bartelt et al. 1985). Nout and Bartlet (1998) assessed attraction of the sap beetle, *Carpophilus humeralis* F. (Coleoptera: Nitidulidae), a pest of corn, to yeast and bacterial volatiles. While no bacterial cultures they tested were attractive to beetles, a variety of volatile emissions from yeast were attractive to *C. humeralis*, and depended on their ability to assimilate and ferment carbohydrates. This attraction is likely relevant to resource locating behavior in the field by the pest. Volatiles produced by *Saccharomyces cerevisiae*, which ferments glucose, sucrose, and maltose, and *Candida shehatae*, which ferments glucose and maltose, were more attractive than volatiles produced by *Candida guilliermondii*, which ferments only glucose. Thus, yeasts with versatile biosynthetic pathways that are capable of digesting complex sugar sources may provide more informative chemical signals to responding insects than yeasts that only ferment a single type of substrate.

Many wood-infesting insects, such as bark beetles and woodborers introduce microbes into trees (Harrington 2005). These microbes can be nutritional symbionts, phytopathogens,

entomopathogens, or mutualists that alter conditions within the host tree, making it favorable for insect colonization. Fungivorous, saprophytic, predatory, or parasitic insects often are attracted to volatile emissions from these microbes, suggesting that microbes influence a larger community than just the beetles that vector them. A recent study by Hulcr et al. (2011) demonstrated that several species of fungus-farming ambrosia beetles were attracted to volatiles produced by symbiotic fungi in olfactometer assays, but not to non-symbiotic saprotrophic fungi. Likewise, the deathwatch beetle, *Xestobium rufovillosum* De Geer (Coleoptera: Anobiidae), is attracted to tree material colonized by wood decaying fungi such as *Coriolus versicolor* and *Donkiospora expansa*. However, non-symbiotic fungi also can be repellant to beetles. Azeem et al. (2013) revealed that MVOCs from the ubiquitous fungus *Penicillium expansum* can actually reduce host settling by the weevil *Hylobius abietis* L. (Coleoptera: Curculionidae), suggesting that some MVOCs may even be useful in integrated pest management approaches.

Hemiptera Many sap-feeding insects have internal microbial symbionts that provide amino acids, sugars and vitamins to their host insects, among other products. Further, there are several examples of insects associating with fungi that sequester fats or sterols, or conversely, microbes may assist the break down cellulose and toxins (Douglas 2009). For instance, some planthoppers (Hemiptera: Delphacidae) (Noda and Koizumi 2003) associate with ascomycetous fungi that improve sterol biosynthesis and nitrogen-recycling (Noda and Koizumi 2003), which indirectly contributes to infochemical synthesis by planthoppers themselves. However, the direct roles of MVOCs as mediators of hemipteran behaviors are not well-studied in comparison with other insect taxa.

One clear example of hemipteran attraction to MVOCs can be found with *Rhodnius prolixus* Stal (Hemiptera: Reguviidae), an important vector of Chagas disease in Central and northern South America. Lorenzo et al. (1999) evaluated electrophysiological responses by *R. prolixus* to volatiles produced from *Saccharomyces cerevisiae* cultures. The electroantennogram results and increased captures obtained with yeast-baited traps demonstrated an attraction by *R. prolixus* to yeast volatiles. However, the authors stopped short of identifying specific semiochemicals from blends of yeast volatile emissions. Similarly, olfactometer assays also were used to demonstrate attraction by another vector of Chagas disease, the haematophagous bug *Triatoma infestans* Laporte (Hemiptera: Reguviidae) to yeast volatiles (Guerenstein et al. 1995).

Environmental Hazards

Few studies have examined the potential for MVOCs to signal hazardous conditions to insects. Phytophagous, predatory, or parasitic insects sometimes are repelled by MVOCs

emitted by infected plants or other potential resources (Steiner et al. 2007a, b). In this case, the effect of microbial colonization on resource quality could be negative for the insect, or the insect may suffer from direct contact with the microbe. Furthermore, environmental hazards signaled by microbial emissions can be a source of evolutionary diversification for insects. For example, Stensmyr et al. (2012) demonstrated that *D. melanogaster* has evolved specific, generically conserved neural pathways for the detection of geosmin, an MVOC produced by potentially harmful microorganisms. Tasin et al. (2012) found that fungal infection by the phytopathogenic fungus, *Botrytis cinerea* reduced both attraction and oviposition by the grapevine moth, *Lobesia botrana* Schiff. (Lepidoptera: Tortricidae), to healthy grapes. Many fungi produce secondary metabolites that are directly toxic to insects (Rohlf and Churchill 2011), and some pathogenic fungi that exploit both dead and living hosts can be highly specialized natural enemies of insects (St. Leger 2008). Additionally, secondary volatile metabolites may help fungi colonize hosts by overcoming insect defense systems (reviewed in Gillespie et al. 2000; Vega et al. 2006).

Entomopathogenic fungi exhibit a diverse array of adaptations that include the general ability to overcome insect immune defenses and alter insect behavior. Two commonly used and best studied entomopathogenic fungi worldwide are *Metarhizium anisopliae* and *Beauveria bassiana*, which produce an array of volatile secondary metabolites. Yanagawa et al. (2011) found termites to have a strong aversion toward the odor of the entomopathogenic *B. bassiana*. Termites apparently can detect potentially harmful concentrations of fungi by olfaction and avoid direct physical contact (Mburu et al. 2012). Hussain et al. (2010) revealed that termites avoided areas treated with cultures of the fungi emanating MVOCs, and repellency largely depended upon specific volatile profiles. Other insects, such as the seven-spot ladybirds *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), also are known to detect and avoid *B. bassiana* volatiles. Collectively, these studies suggest that selection is likely to favor insects that can distinguish hazardous entomopathogens by their volatile profiles, and respond accordingly by avoiding the sources of certain MVOCs. In support of this notion, recent work by Lam et al. (2010) found that female house flies, *Musca domestica* L. (Diptera: Muscidae) detect the presence of harmful entomopathogenic fungi in the odor profile of animal feces, and that females accordingly avoid ovipositing in these resources.

Microbes produce a variety of insect repellents that could contribute to pest control. Azeem et al. (2013) found that the fungus *Penicillium expansum* produced two volatiles, styrene and 3-methylanisole, that reduced the pine weevil, *Hylobius abietis* (L.) attraction to Scots pine twigs. Likewise, endophytic fungi can produce volatile antimicrobial and insecticidal compounds. The endophyte *Muscodor vitigenus* produces naphthalene, which is strongly insecticidal (Daisy et al. 2002).

The leaf beetles, *Oreina* spp. (Coleoptera: Chrysomelidae), have significantly reduced weight, increased development rate, and reduced growth rate when developing in the presence of the phytopathogenic rust *Uromyces cacaliae* (Roder et al. 2007), suggesting reduced plant nutritional quality, or production of toxic fungal metabolites (Hatcher et al. 1995). *Uromyces* on *Rumex* spp. also increases the development time and reduces pupal weight of larval leaf beetles, *Gastrophysa viridula* (Hatcher et al. 1994). However, the presence of *Uromyces* may benefit insect species such as the herbivorous moth, *Lobesia botrana* (Mondy and Corio-Costet 2004). Given these varied effects, the impact of fungal rust infection of plants on herbivore behaviors and performance are deserving of further attention, especially from the perspective of altered volatile emissions from rust-infected plants. For example, it may be the case that insects that are attracted to volatiles from rust-infected plants also contribute to the vectoring of rust fungi to new hosts.

Foltan and Puza (2009) found that volatiles from a nematode-bacteria complex within dead slugs (*Deroceras reticulatum*, Mollusca: Agriolimacidae) or larvae wax moth *Galleria mellonella* (Lepidoptera: Pyralidae) repelled the carabid predator *Pterostichus melanarius* (Coleoptera: Carabidae). The deterrent effect may be important for the survival of the nematode/bacteria complex, or, a mechanism for beetles to avoid potentially infective cadavers. Similarly, Gulcu et al. (2012) found that when a bacteria-nematode complex colonized insect cadavers, they produced MVOCs that repelled ants, wasps, and other foragers that otherwise utilize cadavers.

Generality of Insect Orientation to Microbial Odors

Associations between insects and microorganisms are complex, as they can be disparate, diffuse, and seemingly independent of one another depending on the insect being studied. Assessing the potential impact of insect-microbe associations on insect, plant, or microbial fitness can be cumbersome due to the substantial variability between biological systems. Consequently, generalizations about the function of a particular microbe in a given environment are difficult to make, and the impact of a microbial species on an insect in one system could result in a positive outcome for either parties involved (mutualism), whereas the opposite could be observed in a different system or under different circumstances. Conversely, no effect might be detected at all (Leitner et al. 2010), which is likely the case for most insect-microbe associations.

A common theme reoccurring in insect-microbe chemical ecology studies is that multiple compounds and organisms interact simultaneously. The close association of microbes with other elements in the environment makes it particularly difficult to separate the sources of olfactory cues. Likely,

signaling is bidirectional, if not multidirectional, between microorganisms and insects that are in continual contact with a multitude of bacteria and fungi within their natural habitats, and it is probable that microorganisms can be recovered from almost any insect. A central question in understanding the generality of insect olfactory responses to microbial volatiles is whether the insect recipients of volatile cues from microorganisms perceive them discretely or as a mixture. Given the milieu of microbes and other aromatic elements present in natural ecosystems, individual MVOCs likely are not as informative as blends that advertise complex aspects of habitat suitability.

Microbial Odors in Tritrophic Interactions

In addition to their direct influences on insect behaviors, MVOCs are important components of tritrophic interactions: microbial metabolites may have substantial consequences for insect populations even without directly affecting the behavior of their insect vectors. For example, MVOCs may attract or repel predatory or parasitic insects, provide some degree of protection from harmful microorganisms, or alter insect host selection behaviors. However, studies of MVOCs as tritrophic signals are ecologically complex, and accordingly, relatively few investigators have examined their contribution to insect behaviors. Although there currently is relatively little research on microbially-mediated tritrophic interactions that result from MVOC production, we hypothesize that insect behavioral responses to ambient MVOCs are much more common than currently recognized.

As mentioned above, natural enemies of insects often cue in to plant volatiles associated with insect herbivory and damage, and many comprehensive reviews have been published on natural enemy attraction to plant-induced volatiles associated with insect herbivores (e.g., Engelberth et al. 2004; Turlings and Wackers 2004). However, microbial emissions might improve, alter, mask, or interfere with volatile signals from plants (Boone et al. 2008; Dillion and Dillion 2004; Madden 1968; Pineda et al. 2010). Even mycorrhizal fungi (below-ground fungal symbionts of plants) can impact the production of plant volatiles in response to above ground herbivory (Fontana et al. 2009). Given that plants release a multitude of volatile compounds when attacked by herbivores (Pichersky et al. 2006), locating specific hosts or prey requires natural enemies to decipher specific, highly localized chemical cues (De Moraes et al. 1998; Turlings and Benrey 1998).

These cues can originate from microbial symbionts (Adams and Six 2008; Dicke 1988; Madden 1968; Sullivan and Berisford 2004). Volatiles released by plants under attack by insect-microbial complexes, or volatiles released directly from microbes themselves could provide cues for natural enemies

to discriminate between damaged and undamaged plants (Hulcr et al. 2005), distinguish among herbivore species, and possibly even distinguish intraspecifically among herbivores with different microbial symbionts (Dicke 1999). The influence of microbial symbionts on herbivore populations may be context dependent – benefiting insects by facilitating herbivory, but also negatively affecting insect herbivores by increasing the probability of detection by natural enemies (Thibout et al. 1995). Whether herbivore-induced plants can manipulate entomopathogenic fungi in a manner similar to natural enemies of herbivores (Cory and Hoover 2006; Elliot et al. 2000) remains to be confirmed.

Microbial emissions also can impact insects indirectly in tritrophic systems by providing protective benefits. For example, Lam et al. (2007, 2009) found that metabolites produced by bacterial associates of the house fly served to limit the establishment of entomopathogenic fungi that negatively impact fly reproductive success. Similarly, Davis et al. (2011) found that the bark-beetle associated yeast, *Ogataea pini*, produces volatiles that inhibit the growth of a pathogenic fungus (*B. bassiana*) while promoting the growth of a mutualist (*Entomocorticium* sp. B). However, the role of MVOCs in inhibiting the growth of entomopathogens are rarely explored, and further research should seek to determine how much support can be found for a ‘microbial protection’ hypothesis.

Another important example of a microbially-mediated tritrophic interaction, the ‘vector manipulation hypothesis’ (i.e., host manipulation hypothesis) (George et al. 2013; Ingwell et al. 2012; Mauck et al. 2010; Moore and Gotelli 1990; Poulin 2000), affects insect behaviors both directly and indirectly. For example, Ingwell et al. (2012) found that aphids, *Rhopalosiphum padi* L. (Hemiptera: Aphidae) acquiring *Barley dwarf yellow virus* (BDYV) through *in vitro* feeding exhibited a distinct preference for host barley plants that were uninfected by virus. In contrast, uninfected aphids preferentially selected infected plants. Currently, this apparently is the only study that has directly examined the effect of viral infection on insect host selection behaviors using olfactory stimuli, though Mauck et al. (2010) initially demonstrated this phenomenon with *Myzus persicae* Sulzer (Hemiptera: Aphidae) and *Cucumber mosaic virus* (CMV). Similarly, potato psyllids (*Bactericera cockerelli* Sulc. (Hemiptera: Trioziidae) are a vector for an endosymbiotic α -proteobacteria, ‘*Candidatus Liberibacter solanacearum*’, that is highly pathogenic to potato plants. Davis et al. (2012a, 2012a, b) found that uninfected psyllids preferentially settled and oviposited on plants infected with ‘*Candidatus Liberibacter solanacearum*’ (zebra chip disease), but later defected to uninfected plants once the symbiont had presumably been acquired. Mann et al. (2012) demonstrated a similar tritrophic interaction for the Asian citrus psyllid (*Diaphorini citri*), huanglongbing disease (‘*Candidatus Liberibacter asiaticus*’), and citrus trees (oranges). The studies in this area all have demonstrated that once plants become

infected with insect endosymbionts, they exhibit altered volatile profiles that increase the attractiveness of host plants to uninfected insects (e.g., Davis et al. 2012a, b; Mann et al. 2012; Mauck et al. 2010). Although the impact of viral or bacterial symbionts on host insect fitness is not uniform across these systems, the tendency for substantial shifts in plant volatiles to occur upon infection with endosymbionts appears consistent.

Metabolic Pathways Involved in Microbial Signaling

Many MVOCs are produced during the normal function of energy generation in microorganisms. There are several primary metabolic and biosynthetic pathways that produce secondary metabolites within microorganisms—even within a single species metabolism is versatile.

Pathways

In prokaryotes, three primary pathways of glycolysis exist, and bacteria use one or more of these pathways to dissimilate organic compounds, e.g., sugars, and provide energy; the Embden-Meyerhof pathway, the Entner-Doudoroff pathway, and the Heterolactic (Phosphoketolase) pathway. The overall result of the Embden-Meyerhof (E-M) pathway is the oxidation of glucose into 2 pyruvic acid molecules. It also is commonly utilized by yeast, which reduce pyruvate to alcohol (ethanol) and CO₂. The pathway also is used by lactic acid bacteria to reduce pyruvate to lactic acid. Other bacteria use this pathway as a starting point to produce a wide array of secondary metabolites, such as fatty acids, alcohols, and gases, dependent on the reductive steps subsequent to pyruvate production (Todar 2012). In homolactic fermentation performed by lactic acid bacteria (such as *Lactobacillus*, *Lactococcus*, *Staphylococcus*, and *Streptococci*), lactic acid is the sole end product; whereas in heterolactic acid fermentation, a molecule of pyruvate is converted to lactate and the other to ethanol and carbon dioxide.

Enterobacteriaceae (such as *Escherichia coli*, *Salmonella*, and *Shigella* spp.) can perform mixed acid fermentation resulting in volatile metabolites that are mixtures of ethanol, succinate, and lactic, acetic, and formic acid (Kim and Gadd 2008a). The butanediol fermentation pathways, often employed by bacteria such as *Klebsiella* and *Enterobacter* spp., is similar to mixed acid fermentation, but reduces overall acid formation and results in the production of 2,3 butanediol from pyruvate through formation of a distinctive intermediate, acetoin (Gottschalk 1986a). Butyric acid and butanol-acetone fermentation are used by *Clostridium* spp. to produce butyric acid along with butanol, acetone, acetic acid, CO₂ and H₂ and small amounts of ethanol and isopropanol (Kim and Gadd 2008a).

Propionic acid fermentation is a less common and more complex metabolic pathway performed by propionic acid

bacteria (e.g., *Corynebacteria*, *Propionibacterium*, and *Bifidobacterium* spp.) (Gottschalk 1986a; Kim and Gadd 2008a). These bacteria ferment lactate into acetic acid, CO₂, and propionic acid, all three of which are highly behaviorally active compounds for insects (Hwang et al. 1980; Mukabana et al. 2012). Heterolactic acid bacteria (e.g., *Lactobacillus* and *Leuconostoc* spp.) produce a key enzyme, phosphoketolase, which cleaves pentose phosphate into glyceraldehyde-3-phosphate (GAP) and acetyl phosphate in the heterolactic pathway. GAP then can be converted into lactic acid and acetyl phosphate reduced to ethanol and CO₂ (Kim and Gadd 2008a).

The Entner-Doudoroff (E-D) pathway is a less efficient energy generating variant of the glycolytic pathway that utilizes carbohydrates for respiratory metabolism. It oxidizes glucose into pyruvate and GAP to eventually yield ethanol and CO₂ (Kim and Gadd 2008b). This metabolic pathway is widely distributed in *Pseudomonas* spp., particularly by the yeast-like pseudomonad, *Zymomonas*, and in *Vibrio cholera*. *Zymomonas* bacteria live on the surfaces of plants, and are used in the fermentation of cactus beer, tequila, and mescal, instead of yeast (Obire 2005).

Respiration is a more complex system of primary metabolism that results in the complete oxidation of substrates, such as glucose, by an outside electron acceptor to CO₂ (Gottschalk 1986b; Kim and Gadd 2008a). Glycolysis and four additional components are used: (1) the tricarboxylic acid cycle (or the citric acid cycle) is the oxidation of an organic compound to CO₂; (2) the electron transport system of the plasma membrane that transports substrate electrons through a chain of carriers to a final electron acceptor; (3) an outside electron acceptor, such as O₂ for aerobic respiration, which is reduced to H₂O; and SO₄, S, NO₃, NO₂, fumarate or other inorganic compounds for anaerobic respiration; CO₂ for methanogenesis; and lastly (4) a transmembranous ATPase enzyme (ATP synthetase) to synthesize ATP during the process of oxidative phosphorylation.

Bacterial aliphatic volatiles are formed from fatty acid biosynthetic pathways, whereas aromatic compounds are formed by the shikimate pathway or the degradation of amino acid compounds (Fig. 1). In contrast, nitrogen containing compounds are produced by biosynthesis from amino acids and compounds found widely in nature; but sulfur compounds are generated from dimethylsulfoniopropionate, inorganic sulfides, and lactic acids. Terpenoids are produced primarily from the mevalonate or deoxyxylulose phosphate pathways; and volatiles from halogenated selenium, tellurium, and other metalloid compounds (Schultz and Dickschat 2007). Schultz and Dickschat (2007) described almost 350 MVOCs released from bacteria, and they estimate that 50–80 % of the bacteria that they investigated in their lab produced volatiles; however the functions of the volatiles in terms of effects on the organism's life history remain largely unstudied. The compounds emitted

from the most widespread species of bacteria were determined to be pyrazines, sulfurs, geosmin, and 2-methylisoborneol, and the array of compounds produced by even a single microbial species can be substantial. For example, Filipiak et al. (2012) identified 32 and 37 MVOCs, respectively, from *Staphylococcus aureus* and *Pseudomonas aeruginosa*.

Both primary and secondary metabolic processes result in a diverse variety of volatiles produced from an extensive phylogenetic array of species living in varied habitats, from aquatic to enteric to terrestrial. While primary metabolism focuses on the essential production of cellular components, such as DNA and amino and fatty acids, secondary metabolism consists of subsequent downstream reactions. The production of secondary metabolites often is species-specific or restricted to a limited phylogenetic group, and secondary metabolites produced by microbial species may be more relevant to insect chemoreception than end-products of primary metabolism.

Phenological and Environmental Effects

The induction of secondary metabolic products can differ depending on the phenological stage of the microorganism and environmental conditions, such as availability of nutrients, moisture, temperature, ambient volatile organic compounds (VOCs), and the local microbial community composition (Korpi et al. 2009). For example, *Stenotrophomonas rhizophila* released different quantities of MVOCs when grown on nutrient broth with and without glucose, as well as when bacteria were in different growth phases (Kai et al. 2009b). This study demonstrates how highly interconnected environmental factors are with the metabolic pathways utilized by microbes, which subsequently mediates the array of MVOCs produced. If, as presented in this review, MVOCs have influence on insect behaviors such as attraction, repulsion, selection of oviposition sites, and location of nutrient resources; then a particular suite of MVOCs could potentially shape local insect species community structure through downstream interkingdom communication.

The production of secondary metabolites also has a temporal aspect. For instance, when a bacterium first colonizes a freshly deceased animal, it finds itself in a nutrient-rich environment. In this situation, most bacteria employ primary metabolism that enhances growth and facilitates reproduction as high priority functions (Vining 1990). However, as the ephemeral resource and its nutrients are depleted, the bacterium utilizes other strategies and begins activating lower priority pathways that indirectly promote survival or are useful to metabolize alternative substances as energy sources and produce unique secondary metabolites. This aspect of timing should be considered when sampling MVOCs in a field study. In a nutrient-rich environment, the microbe produces a particular VOC profile that corresponds to stress-free growth, but under conditions of competition or in a nutrient-limited, or

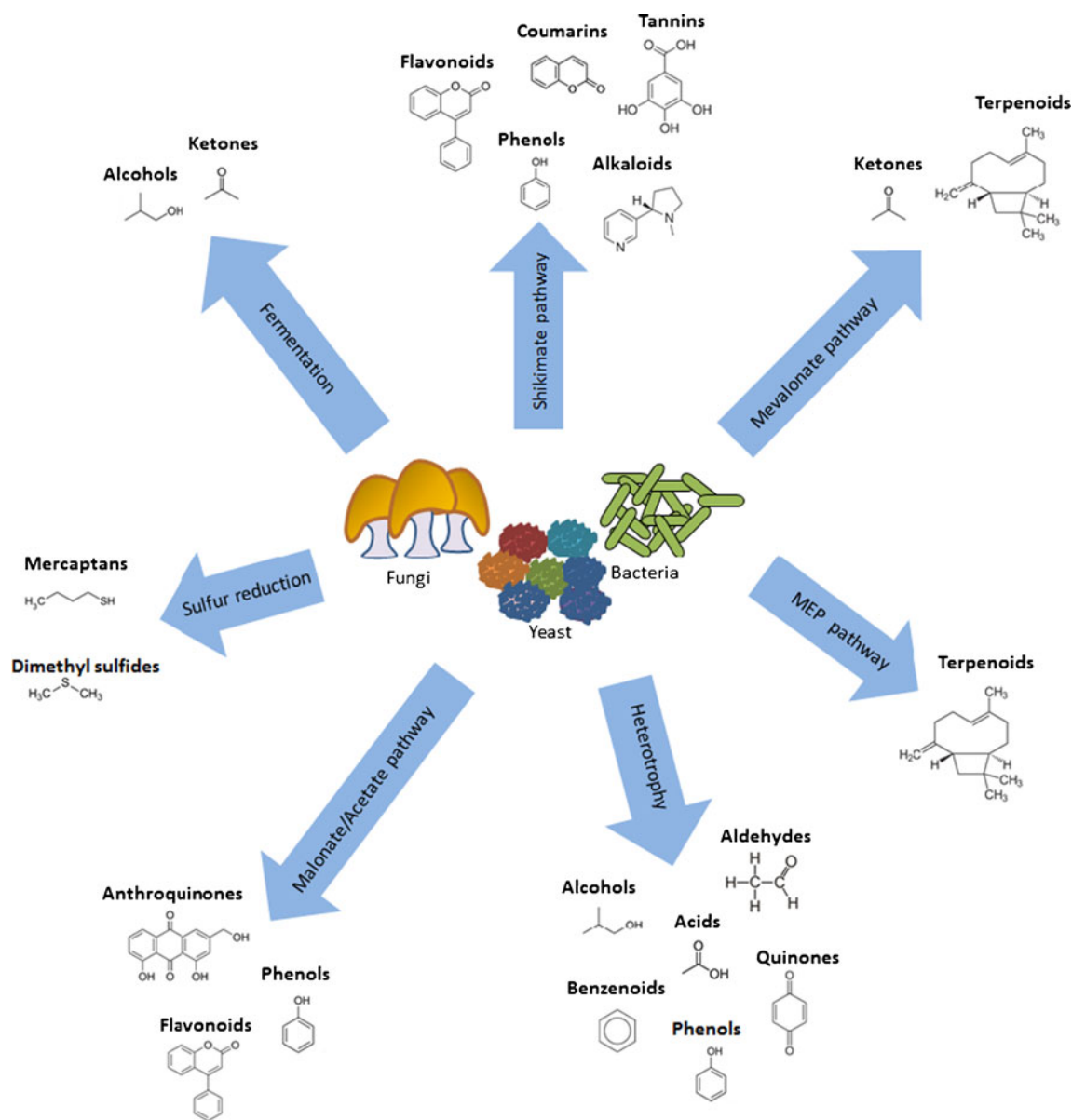


Fig. 1 Several important metabolic pathways utilized by bacteria and fungi, and classes of end-product volatiles that have ecological relevance to insects. Although microbial metabolic pathways and resulting

secondary metabolites are numerous and diverse, the pathways and end-products pictured here are among the most prevalent in the insect semiochemical literature. MEP: Methylerythritol phosphate

otherwise stressed environment, a different suite of MVOCs may be produced as the metabolic pathways shift to enable adaptation to changing resource availabilities. Alternatively, as decomposition progresses, some microbes may not possess the metabolic pathways necessary to utilize the changing resource and are replaced by species that possess the necessary metabolic pathways, thus resulting in a fluctuating microbial community structure and with it, a shifting volatile profile.

For instance, it is known that insects respond to VOCs released by cadavers. Von Hoermann et al. (2011) investigated VOCs emitted from pig carcasses that were attractive to hide beetles, *Dermestes maculatus* (De Geer) (Coleoptera: Dermestidae), during various stages of decay. They

determined the beetles were most attracted to the carcass during the post-bloat stage corresponding with the significant production of benzyl butyrate during that stage. Benzyl butyrate is derived from butyric acid (Zhang et al. 2009), a product of anaerobic fermentation, such as that occurring in the colon by heterotrophic bacterium *Clostridium butyricum* (Popoff 1984). Burying beetles *Nicrophorus vespillo* (Linnaeus) and *N. vespilloides* Herbst (Coleoptera: Silphidae) responded to distinct odors of sulfur-containing VOCs (e.g., dimethyl sulphide, dimethyl disulfide, and dimethyl trisulfide) commonly emitted by fresh vertebrate carcasses (Kalinová et al. 2009). The metabolism of sulfur containing amino acids, cysteine and methionine, leading to

the emission of sulfur containing VOCs can occur in several bacterial genera that inhabited the carcasses, e.g., *Brevibacterium*, *Corynebacterium*, *Micrococcus*, *Staphylococcus*, *Arthrobacter*, and lactic acid bacteria (Schultz and Dickschat 2007).

It is not always known what specific organisms or chemical processes are contributing to VOC production. However, insects appear to recognize unique time-based MVOC profiles and use them to determine if a resource is suitable; thus MVOCs may provide cues related to temporal aspects of habitat suitability. This notion is supported by the findings of Chaudhury et al. (2010), who demonstrated that MVOCs from a mix of *Enterobacteriaceae* isolated from wounds infested with the screwworm, *Cochliomyia hominivorax* (Coquerel) (Diptera: Calliphoridae) attracted gravid females for oviposition significantly more effectively after 48 hr and 72 hr of growth in blood than at 24 hr or 96 hr.

Eukaryotic Fungi

In addition to prokaryotes, eukaryotic 'microorganisms' such as fungi are important producers of volatile emissions (Faldt et al. 1999; Morath et al. 2012; Raguso and Roy 1998; Steinebrunner et al. 2008). Fungi are decomposers that breakdown dead plant and animal materials via unique and varied biochemical pathways. Fungi utilize many of the same primary energy exchange reactions as bacterial microorganisms: carbon energy metabolism by glycolysis, fermentation, and respiration; and nitrogen and sulfur metabolism (Hutchison 1973). Fungi feature prominently in the carbon cycle, during the process of decomposition in soil. They are crucial in biosynthesis of complex organic material, such as cellulose, lignin, polysaccharides, and proteins, into simple sugars, peptides, and amino acids and ultimately into the end products CO₂, H₂O, NH₃, H₂S, and H₂. Fungal molds and yeasts are primarily aerobic, terrestrial organisms that utilize organic compounds for growth. However, yeast can grow anaerobically via the use of fermentation and play a role in fermentation of high sugar environments. A tremendous amount of work has been done on yeasts and their production of ethanol (Sun and Cheng 2002), acetone (Green 2011), acetaldehyde (Romano et al. 1994), and other metabolites for use in the food and energy industries (Alper et al. 2006; Bekatorou et al. 2006). Yeasts utilize both types of chemoorganotrophic metabolism, fermentation and respiration, to obtain energy. *Saccharomyces* produces acetaldehyde, ethyl acetate, ethanol, n-propanol, isobutanol and isopentanol gases (Hutchison 1973) which can produce effects on other fungi, such as growth inhibition, dependent on concentrations present. Furthermore, these compounds are known to directly affect insect behaviors and play a role in feeding attraction, particularly isobutanol and acetaldehyde (Landolt 1998). In addition, some fungi are facultative

anaerobes, particularly those that inhabit the deeper layers of soil where high CO₂ and low O₂ environments exist (Cheng et al. 2012). Thus, emissions from subterranean fungi also may influence the behaviors of soil-dwelling insects (Bengtsson et al. 1988; Konate et al., 2003).

Fungi utilize a wide range of reaction types during secondary metabolism and they can produce a multitude of aromatic secondary metabolites, the most abundant of which are the polyketides (Crawford et al. 2009; Keller et al. 2005). These secondary products in fungi are not essential for growth and reproductive metabolism, and they have diverse structures and activities. They are often distinctive products produced by individual organisms or particular groups of organisms that appear to have a range of bioactivities as opposed to a single function (Vining 1990). Most are small oligomers, the majority of which are excreted from the organism into their surroundings. A review by Pelaez (2004) surveyed the literature between 1993 and 2001 and found more than 1500 fungal metabolites with described biological activity. Those activities included antibacterial, antifungal and antitumor compounds derived from a small number of basic metabolic pathways that utilize primarily polyketides, nonribosomal peptides, and terpenoids.

Polyketides are carbon chains of differing lengths synthesized by the interaction of multidomain proteins similar to eukaryotic fatty-acid synthases, called polyketide synthases, and short chain carboxylic acids, such as acetyl CoA and malonyl CoA. Terpenes are one example of a polyketide, and often are represented by plant metabolites known to be odoriferous, such as camphor or turpentine. They are composed of linear or circular, saturated or unsaturated isoprene units, whereas indole alkaloids are usually derived from amino acids (e.g. tryptophan) and dimethylallyl pyrophosphate. As many secondary MVOCs have been shown to have direct effects on the behavior of receiving species, they likely benefit aspects of the survival and proliferation of the responding organism (reviewed in Kai et al. 2009a; Stotzky and Schenck 1976; Vining 1990). However, most functions of bacterial and fungal secondary metabolites are as yet undiscovered.

Summary and Future Direction

The cosmopolitan distribution of microorganisms creates a context for frequent insect exposure and response to microbial species. The relative ubiquity of insect-microbe associations likely indicates that the effects of MVOCs on insect behavior are more prevalent than currently recognized, and that interkingdom signaling from microbial sources may play a substantial and often overlooked role in insect behavioral ecology (Frago et al. 2012). Here, we have provided one of the first syntheses of the literature pertaining to the effects of MVOCs on insect behaviors, (but see also Leroy

et al. 2011a), discussing the generality and ecological roles of MVOCs as insect semiochemicals, as well as some of the biochemical pathways involved in MVOC production.

Most studies we reviewed dealt with microbial volatiles as indicators of food sources, oviposition sites, mating opportunities, and signals of environmental suitability or potential hazards. Although there are various examples of tritrophic interactions resulting from MVOC production by symbionts of herbivores, more research in this area is needed. In addition, the indirect effects of microbial activity on volatile emissions from plants and animals can have striking effects on insect host selection behaviors. There is evidence to suggest that microbial mediation of plant and animal volatile emissions may be involved with the introduction or dispersal of microbes to new habitats, although there currently is a limited conceptual framework for this notion. However, there remains the possibility that many of these responses are incidental, and that natural selection tends to promote weakly positive, diffuse ecological interactions (Six and Wingfield 2011).

The biochemical pathways involved in the production of microbial secondary metabolites and infochemicals are diverse and complex. In general, there is a moderate degree of functional redundancy in MVOCs from microorganisms, which may reflect overlapping biochemical pathways for volatile production within biological systems. However, emission rates, the ratio (blend) of compounds present in microbial headspace, or a combination of these factors likely supersede the importance of any single compound as infochemicals. Fungal tissues commonly produce polyketides and short-chain alcohols, whereas bacterial tissues tend to be more commonly associated with amines and pyrazines. However, there is an incredible diversity of secondary metabolites produced by microorganisms that may have important behavioral consequences for insects. As of yet, only a small fraction of MVOCs have been assayed as insect semiochemicals, and relatively little is understood about the ecology and evolution of insect attraction to MVOCs.

It will be important for future studies in this emerging subfield of chemical ecology to approach the effects of MVOCs on insect behaviors from a systematic perspective. Foremost, it will be relevant to distinguish which components of plant or animal volatile emissions may actually be due to microbial metabolism. For example, some components of floral scent may be due to microorganisms (Herrera et al. 2008; Raguso 2008). Thus, reports in the scientific literature prior to the advent of modern analytical and molecular techniques, may incorrectly characterize compounds as floral odors when the floral bouquet is in actuality a combination of both floral and microbial odors. With this in mind, we suggest that future studies of insect chemical ecology consider a 'microbial' alternate hypothesis, and researchers should be careful to rule out bacteria, fungi, and their effects on plant and animal emissions, as sources of volatiles.

Another important consideration will be to distinguish whether insect responses to microbial emissions are learned behaviors, genetically conserved traits, or some combination of both these factors. Furthermore, there will remain a need to establish the general impetus for insect responses to microbial emissions; that is, are insects responding to microbial emissions in search of food, mates or oviposition sites? Or conversely, are microbial emissions providing important cues regarding habitat suitability? An additional key consideration for entomologists studying insect responses to MVOCs is the identification of the microorganisms that insects are responding to by using modern molecular techniques, as morphological traits alone often are not sufficient for identification of many microorganisms. Inconsistency by researchers in either of these areas could lead to an incorrect interpretation of experimental work.

As in Davis et al. (2011), we propose here several hypotheses for researchers to consider as they investigate insect associations with microbial emissions. (1) The semiochemical hypothesis: MVOCs serve as chemical signals that provide critical information regarding habitat suitability, the nutritional quality of host substrate, oviposition sites, or mating opportunities; (2) The protection hypothesis: MVOCs actively suppress the growth of harmful microorganisms, or repel predators or parasitoids; (3) The manipulation hypothesis: infection of host substrates by microorganisms acts to increase or reduce the attractiveness of the substrate; and finally, (4) The neutral hypothesis: chemical emissions from microbial sources influence insect behaviors by coincidence, potentially as a result of similarity to evolutionarily relevant infochemicals. There are doubtless other testable hypotheses that could emerge from this review, and it is notable that only hypothesis (1) relates to direct interactions between insects and MVOCs – the possibilities for indirect associations between insect behaviors and MVOCs are conceivably inexhaustible. However, the above hypotheses represent a concrete starting point for widespread investigation of ecologically important associations between insects and MVOCs.

Microorganisms are ubiquitous in most ecosystems, and until recently the incredible complexity introduced to the field of entomology by microbial players has been scarcely explored. Advances in modern analytical and laboratory techniques are allowing researchers to peer ever further into the true complexity of insect-microbe associations, and it is apparent that the influence of microbial metabolic activity on the behavior of higher organisms is profound. We predict that links between insect behaviors and MVOCs could be as productive a field of exploration as insect responses to plant emissions, and indeed, further research may well demonstrate that the two phenomena are in fact integrated in nature.

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